H. C. Perkins.

MEMOIRS

OF THE

PEABODY ACADEMY OF SCIENCE.

VOLUME I. NUMBER II.

Case

SALEM, MASS.
PUBLISHED BY THE ACADEMY.
MARCH, 1871.

THE SALEM PRESS; F. W. PUTNAM, PROPRIETOR.

PEABODY ACADEMY OF SCIENCE.

SECOND MEMOIR.

EMBRYOLOGICAL STUDIES

ON

Diplax, Perithemis, and the Thysanurous Genus Isotoma.

BY

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1871.

ACCEPTED FOR PUBLICATION

JULY, 1870.

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ON

DIPLAX, PERITHEMIS, AND ISOTOMA.

THE DEVELOPMENT OF DIPLAX.*

THE eggs of a species of this genus were found July 2d by Mr. A. Hyatt, attached to the leaves of a submerged sedge. The nidus, evidently (as suggested to me by my friend Dr. Hagen) too large to have been laid by a single dragon-fly, consisted of a long ropy mass of a gelatinous consistency, about a quarter of an inch thick, which twined about the leaves of the grass. Through this mass the eggs were thickly dispersed. They must have been laid for a week or more, as on the 16th of July large numbers had already hatched out. They continued to hatch while in glass jars, till the first week of September, those eggs situated in the middle of the gelatinous mass seeming to hatch last; in this way a succession of young dragon-flies was disclosed through the summer. I was unable to carry them farther on in their development, and did not learn what species they belonged to.

The eggs are oval, cylindrical, .03 of an inch in length, and about half as thick. Some were observed to be contained in an ovate, transparent, gelatinous envelope, about twice the size of the egg itself, and at the anterior pole contracted into a short neck (Pl. 1, fig. 3). On some eggs was observed a tubercle attached to the anterior pole of the shell, and retained quite late in embryonic life, as in Pl. 2, fig. 13, *t*.

In all the eggs observed the blastoderm had apparently been formed, the blastodermic cells having disappeared. Such eggs (Pl. 1, fig. 1, 1*a*) presented a clear space around the periphery of the egg, the yolk-mass being formed of granules of very unequal size. At this stage (fig. 1), the granules are massed more towards what is probably the posterior pole of the egg. In the next stage observed (Pl. 1, fig. 2, 2*a*), the

*Nearly all the drawings referring to Diplax, and which give this chapter most of its value, were made under my direction by Mr. J. H. Emerton, the eggs illustrating the points I wished to describe, having been, in most cases, selected for him to draw. A part of the article, especially that relating to the revolution of the embryo, is described from his drawings, as I did not observe it.

position of the embryo is internal to the yolk, being surrounded by a layer of embryonal cells; the rudimentary body and limbs floating in the middle of the egg. The cephalic lobes are partially developed, forming an obtusely rounded mass projecting from the yolk, and situated nearer the middle of the egg than in the next stage. The cephalic lobes overhang the base of the antennal rudiments, indicating that these lobes belong to the antennal ring, being probably the tergal portion. The appendages of the head and abdomen have budded out, and are grouped into two masses, *i.e.* the mouth-parts (fig. 2, I–IV), and the thoracic appendages (fig. 2, V–VII).. Of the remainder of the body only the ventral wall (sternites) of the head, the thorax, and two basal abdominal segments appear. The sternites of the first and second maxillary segments are now distinct, and exactly the same in size and development as those of the thorax or abdomen, and as they disappear in after life, their appearance at this stage is worthy of note, as indicating that the segments composing the head are in the embryo exactly like those of the thorax or abdomen, and, so to speak, of the same rank, not being, as some authors have believed, subsegments. When, at a latter stage, the tergal walls of the cephalic segments are completed, we have in each arthromere of the head, a ring nearly as perfect as in the thorax. In after growth, the sternal portion of the arthromere is the first to be absorbed, by the approximation of the base of the cephalic appendages on the median line of the head.

Seen from beneath (Pl. 1, fig. 2*a*), the antennæ, mandibles, and first maxillæ form a group by themselves, while the second maxillæ (labium) are turned backwards and grouped with the legs.

The development of the abdomen is, then, later than that of the head and thorax, the development of the germ progressing from the head backwards. The extremity of the abdomen was not detected, though I have no doubt but that farther and more skilled observation would have enabled me to see it.

The mandibles are from this point of view short, thick, and appear to arise just beneath the base of the antennæ. The maxillæ are twice as large as the mandibles and one-half the size of the labium. They are broad at base, and situated much farther apart than the mandibles. The second maxillæ are twice the size of the first pair of maxillæ, and one half as large as the first pair of legs. The bases of the two appendages are far apart, in this respect also corresponding with the thoracic appendages. They are bent inwards in the middle, and their extremities reach near to the middle of the first pair of legs. The three pairs of legs are almost exactly similar in size, and are inserted at nearly equal distances apart. They are folded upon the ventral side of the body, and are long enough to be bent inwards at nearly right angles, so that the extremities nearly meet over the median line of the body.

In the next stage (Pl. 1, fig. 4) the rudiments of the eyes appear, the head having enlarged and approached nearer the anterior end of the egg. The appendages of the head are much the same, the antennæ, however, being a little longer, and the second maxillæ (labium) are considerably longer, but still in their position associated with the legs. These latter have grown longer, and are laid along the side of the body, underlapping each other; the hind pair are the longest and are bent upwards at their extremities. The abdomen is now clearly sketched out, forming a broad obtuse lobe incurved at the tip, and bent beneath the body, with traces of four segments.

I will now describe more fully the changes undergone during this period. August 25th, the embryo had assumed the form indicated by Plates 1, 2, figures 5, 6, and my remarks regarding this period are mostly suggested by the faithful studies of Mr. Emerton, as I did not myself observe the revolution of the embryo. Figure 5 (though a little upturned, giving a partial view from beneath, and showing very finely the relative positions and attachments of the limbs and mouth-parts) represents the embryo in its usual position, seen laterally and previous to revolving in the egg. The head is not distinctly separated from the thorax, the tergites not being visible, while those (t''') of the postabdomen (*pat*), as we may call the temporary subdivision of the abdomen, are clearly marked out. The clypeus (*c*) is prominent, and, in the position here given, nearly reaches to the ends of the antennæ. The antennæ are about a third longer than the mandibles and maxillæ, which are both very equal in size. The position of the labium is interesting as showing that even in the embryo of insects the second pair of maxillæ are intermediate in position and form between the first maxillæ and the legs. The temporary postabdomen, so well marked in this stage, may be said to represent the permanent postabdomen of the macrurous Crustacea. The body is cylindrical, oval, the head is very small in proportion to the rest of the body, the thorax forming about one half the bulk of the body. The two terminal lobes of the eleventh abdominal segments are large and conical in form. The mode of development and relation of the rudiments of the eleventh ring to these lobes will be interesting to trace hereafter. The sternites (*st*) are now indicated, and the rudiments of the intestine (*i*) first appear in the postabdomen.

Two days later, August 27th (fig. 6*b*), an embryo was observed rolled on itself and placed across the shorter diameter of the egg. This and figures 6, 6*a*, 7, evidently represent the embryo in the process of turning; up to this time the head has laid in the posterior pole. Figures 8 and 8*a* represent the embryo after it has assumed its final position, with the head in the anterior pole of the egg. The bulk of the head as compared with that of the rest of the body is well shown. A slight indentation marks the base of the clypeus, the front edge lying between

the antennæ. The ventral walls are well developed between the rudimentary appendages. A day after, August 28th, the embryo still mostly rolled upon itself, presents more of a dorsal aspect, and the postabdomen (*pat*) is brought out more in relief, showing the dark central spot, or rudiments of the intestine (*i*). The legs are a little farther along in their development, and the thickening of the ventral walls, or sternites (or perhaps the rudiments of both sternites and pleurites, the two not having yet been differentiated), is more marked, the region seeming to widen and extend higher up the sides of the body. The sutures between the sternites are also well indicated.

In an embryo observed August 28th, the body is unrolled and lies nearly straight in the egg. The broad and short vertex of the head shows a broad plano-convex, transversely narrow, oblong area, at each side of which the eyes form a dark rounded oval spot. The yolk mass fills up the bulk of the body. The arthromeres are plainly indicated, but no sutures are apparent. Those defining the segments of the postabdomen are however clearly seen, the four basal joints being well shown ventrally, while the free postabdomen is upcurved, the tergites being distinct. The rudiments of the intestine have extended along the whole length from the anal extremity, which begins between the terminal lobes, and extends to near the base. The central darker mass is perhaps the rudiments of the anal plexus of tracheæ, where the blood is to be aërated.

A ventral view shows the broad sternal area, on the edges of which the appendages overlap. The head is nearly as broad as the rest of the body. The antennæ are inserted near to, and opposite, the eyes, their tips nearly meeting, and extending opposite the first maxillæ. The second maxillæ do not appear, from this view of the body, to greatly exceed the size of the first pair, and are grouped with them. The form of the postabdomen, with the rudimentary intestine, is much as when seen from above.

The same specimen seen two days later, August 30th (fig. 6*a*), has changed but slightly though it shows distinctly the base of the postabdomen, and the number of segments composing the abdomen. If we are right in supposing that the ring marked 1 is the basal segment of the abdomen, then the body of the abdomen consists of six well marked segments, and the small slender postabdomen consists of five segments, making eleven in all. The anal stylets hence appear to belong to the eleventh segment. Later in this (8*a*) stage the bases of the stylets are retracted, as it were, within the tenth ring so as to appear appended to it, and the eleventh segment is only represented by a small tergite. The anal stylets therefore in this genus, and undoubtedly in the Libellulidæ generally, must be considered as appendages to the eleventh abdominal segment.

In this drawing only the base of the antennæ is visible, the remainder

being laid along the middle of the body. The second maxillæ are still bent backward and resemble the legs, the tips being still simply rounded.

In figure 7 the embryo is observed lying across the egg, showing the opposite side of the embryo to what is shown in figure 6. The post-abdomen is still free from the body, which is rolled closely on itself, so as to show very distinctly the insertion of the appendages.

The bulk of the head is about the same. The antennæ (1) have become more differentiated, being slenderer and inserted much higher up and above the middle of the head so far as shown by the drawing. The eyes are nearer the base of the head, and nearer the vertex than before. The mandibles and maxillæ have apparently remained the same.

In the second maxillæ the changes are most interesting. The outer edge of the tip of each limb is produced into a point, while the tip itself is somewhat square. The two limbs are however separate, and still grouped with the legs, though directed more anteriorly than in the previous stages. The insertions of the legs seem obscured by the yolk mass overlapping and extending nearly to the middle of them.

Comparing the stage indicated by figures 6 and 7 with the previous one (fig. 5), the principal changes are these: the body from being oblong oval has greatly thickened so as to become almost spherical, though it afterwards, at a period preceding that represented by figures 8, 8*a*, becomes oval again; the head has grown larger in proportion to the bulk of its appendages; this is due to the more rapid growth of the parts between the base of the appendages and the eyes. Two more abdominal segments have been added, both apparently at the base of the postabdomen. As in the Myriapods (Julus) and worms, increase in the number of segments seems to take place near the terminal segment of the abdomen. Another important change is the concentration of the yolk towards the back. In a little more advanced stage (fig. 7*a*) than represented by figure 7, the embryo has assumed a longitudinal position in relation to the egg, the head pressing against the anterior end of the egg. The second maxillæ are longer and intermediate in form between what is indicated by figures 7 and 8. The end of the abdomen is more advanced, the tip being acute and ending in rudiments of bristles arising from the anal stylets. The rudimentary eyes consist of seven large epithelial cells of irregular shape surrounding a central larger one, and situated on a distinct piece of the head, indicated by the dotted line in the figure, dividing the clypeus from the epicranium. The labrum is distinct and separated from the clypeus by a suture. The legs are also considerably longer than in figure 7.

At the next stage (figs. 8, 8*a*) the body is more elongated, the head is larger, and the anal stylets are fully formed, the rudiments of the setæ being more apparent than before, while the yolk mass is still more circumscribed.

The head now occupies the anterior fourth of the egg. The eye-bearing piece of the epicranium now stands out; its lower edge is distinct from and overlaps the base of the mandibles (this not shown in the figure) but merges insensibly into the clypeus, there being no suture between, though there is apparently a slight depression where the clypeus seems to join with the eye-bearing piece. The clypeus is quite large and well developed, being clearly defined and separated by a well marked suture from the labrum. The labrum (fig. 8, *lb*) seen sidewise appears somewhat scoop-shaped and resembles in form that of the cricket, the outer edge, when seen laterally, being slightly curved, the inner very convex. The antennæ show no signs of articulations and are filled with fine granules. They are slenderer and (fig. 8, I) twice as long as the mandibles, and curved around so as to just touch the ends of the maxillæ (fig. 8*b*, III), impinging on the second maxillæ. The mandibles are directed a little obliquely backwards, but are not curved, and no appearance of teeth can yet be detected. The first maxillæ are a little longer than the mandibles, their insertion, or base, being higher up, and the ends extending a little beyond. The origin of the second maxillæ (fig. 8, IV) could not be made out; it appeared to be below that of the first maxillæ. They are now evidently grouped with the other cephalic appendages, and are no longer so plainly associated with the legs as in the previous stages. They are nearly four times the bulk of the first maxillæ. There is a constriction beyond the middle, beyond which the appendage again bulges out, and the tip is somewhat truncated.

The postabdomen is nearly as bulky as the head, the tip of the anal stylets reaching half way to the middle of the egg. The stylets are nearly equal in size. They are not articulated, and end very acutely, the outermost being the longer and slenderer. The figure shows their relation to the abdomen. The rudiment of the terminal bristle is seen on the outer stylet. The large nervous ganglia (fig. 8, *n*) are seen laterally to be nearly square, very approximate, the commissures being very short.

Two days later, the specimen being observed July 27th, the second maxillæ approached each other and the sides were closely appressed, taking on somewhat the form indicated in figure 8*a*, thus forming the labium, with its tip touching the ends of the anal stylets. The tip of each second maxilla is square, where before it was subacute and cylindrical. The mandibles and first maxillæ remain unchanged, no signs of the terminal teeth of the mandibles being visible. The antennæ are, however, much longer and slenderer, the tips reaching beyond the middle of the labium. The eyes are more distinct, are larger, and formed of dermal scale-like cells. The abdominal segments have become more distinct. The legs have grown longer and are better defined, the articulations beginning to appear.

Another embryo, observed July 27th, had reached about the same stage

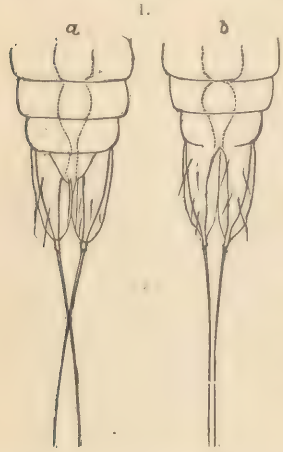
of growth. The cephalic lobes, including the antennary segment, have assumed much more of the form as seen in the mature larva. The entire head is divided into two very distinct regions, *i.e.*, one before the mouth-opening (*preoral*, including the clypeus and labrum, and antennary, or first segment of the head), and the other behind the mouth (*post-oral*, including the mandibular or second segment, the first maxillary or third segment, and the labial, second maxillary or fourth cephalic segment).

At this period the embryo is quite fully formed and is about ready to leave the egg. The three regions of the body are well defined. The articulations of the tergum have become apparent. The body is so bent on itself that the extremities of the second maxillæ just overlap the tip of the abdomen. The front of the head is now still farther differentiated. The supraclypeal piece seems to be merged into the antennary ring, the sutures between them having disappeared. The antennæ are inserted higher up, just in front of the eyes, or rather the eyes have, as it were, dropped down. The clypeus is broad and large, and the slightly bilobate labrum is separated from it by a suture. The mandibles and first maxillæ are still tubercular in shape, the teeth of the former not yet appearing. The two halves of the labium are now placed side by side, with the prominent spinous appendage on the outer edge of each side of the tip. These spines are probably the rudiments of the labial, or second maxillary palpi, not afterwards developed, but as seen in figure 8*b*, forming inarticulate spines, or, as in the adult larva of this family, stout, curved, raptorial hooks. The legs are long and partially bent back on themselves, and at the angles the articulations begin to appear. The coxo-femoral joints are very distinct; the tarsi are directed upwards, and the two claws in which they terminate are simple, straight, and equal in size. The tip of the abdomen ends in two unequal pairs of stylets, terminating each in a long bristle.

On removing the embryo from the egg when a little farther advanced (fig. 9, observed August 16th), and on straightening the body out and viewing it laterally, we are strikingly reminded of the general form of the Lepismæ, and the inference is strongly suggested that they are embryonic, degraded Neuroptera, and should therefore probably be considered as a division standing at the foot of that suborder. The resemblance is still carried out when we examine the shape of the head, the shape of the mandibles (better seen however at a subsequent stage), the homonymous rings of the body, and the form of the end of the abdomen, with the small terminal tergite resting between the large terminal spines tipped with a long bristle, thus resembling the abdominal tip of Lepisma. Cut 1, *a* is a dorsal, and *b* is a ventral, view of the end of the abdomen at this stage. The rudimentary eleventh ring is represented by a triangular supra-anal piece, or plate (corresponding to the supra-anal plate, as we are accustomed to call it, of other Neuropterous

larvæ, and of Lepidopterous larvæ). Its base overhangs the base of the two pairs of anal stylets. Of these latter the upper pair are lamellar, and broad, and rounded at the end; the lower pair are cylindrical and long and slender, bearing each a long straight bristle, twice as long as the stylet itself. Comparing the end of the abdomen of this embryo with the same parts in the recently hatched larva (see cut 3, y) the four stylets are seen in the latter to have been shortened to serve as anal valves, and the bristles are still shorter. These stylets in the larva appear to be appendages of the tenth segment.

1.



The head is large, and the body gradually tapers from it to the end of the abdomen, and is flattened, especially the abdomen. The head is divided into two divisions, indicated by a suture leading from the vertex to the base of the first maxillæ, thus separating the occiput (fig. 9, 4) from the epicranium, and showing that the occiput, or that part of the head behind the eyes and insertion of the antennæ in adult insects, is the most posterior part of the head, and is the tergite of the labial, or second maxillary segment. The eyes now consist of an irregular group of rudely formed facets, and remind us of the few large facets forming the eye of the Lepismidæ. The antennæ are inserted in front of and a little below the eyes, and consist of three joints. The mandibles and maxillæ are of the same size and form as before, while the labium (second maxillæ) is appressed to the under side of the body, and reaches as far back as the insertion of the hindermost pair of legs. The long slender legs once bent at the coxo-femoral joint, reach, when laid along the body, to the middle of the tenth abdominal ring. The tergite of the eleventh ring (fig. 9) is now distinct, forming a short triangular piece resting upon the base of the large stout terminal spines destined to form the anal valves of the free swimming larva (cuts 2, 3, y) where, however, they are very much shorter.

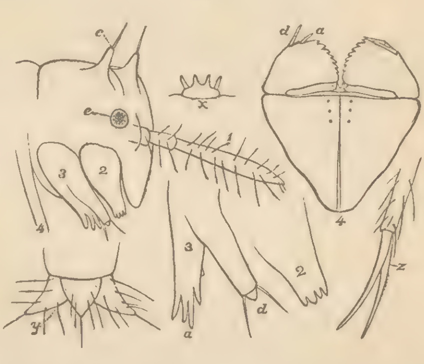
2.

The nervous system (fig. 9, *n*) is now proportionally smaller than before, the ganglia being oval in outline, seen laterally. The intestinal canal is now formed, and at *x* is surrounded by a plexus of tracheæ, in which the main tracheæ (*t*) terminate. The main branches of the tracheæ form a terminal loop in the head. The yolk mass is now much restricted, being confined to the labial segment of the head and the thoracic segments. Figure 12 shows the earliest form of the tracheæ to consist of two main trunks giving off lateral twigs at nearly right angles, forming a loop opposite the second pair of legs, and bifurcating (fig. 9) in the head. The twigs at the posterior termination form the respiratory plexus.

At a subsequent period in the life of the embryo (fig. 10, observed July 25th), upon removing an embryo from the egg, the principal change is in the labium, which is now comparatively shorter than before, and is drawn up nearer the front of the head, thus standing out freer from the body than before; the articulations in the antennæ and legs are more distinct, and the edges of the eyes are better defined.

On the same day (July 25th), another embryo (fig. 11) was taken from the egg, apparently being just ready to hatch. The principal change that has occurred is in the position of the second maxillæ, which now stand out at nearly right angles from the head, while the mandibles are dentate at the end, and remind us of the shape of the mandibles in Lepisma. The head is also freer from the body. The labium is distinctly bilobate, and the occiput is separated by a well defined suture from the epicranium. The labium (second maxillæ) is now broad, flat seen from above, oblong in shape, square at the end, with the rudiments of the palpi (fig. 8*b*). The body is covered with minute tubercles, which in the next, or free swimming stage, give rise to hairs.

3.*



The Larva (cuts 2 and 3). When hatched it is .05 of an inch in length. The head is now free and the antennæ stand out free from the

* Cut 3. Side view of the head of the larva of Diplax before the first moult; *c*, deciduous tubercles terminating in a slender stylet; their use is unknown; they have not been observed in the full-grown larva; *e*, the compound eyes. 1, the three jointed antennæ, the terminal joint nearly three times as long as the two basal ones. 2, the mandibles, and also enlarged, showing the cutting edge divided into four teeth. 3, maxilla dividing into two lobes; *d*, the outer and anterior lobe, 2-jointed, the basal joint terminating in two setæ; and *a*, the inner lobe concealed from view, in its natural position, by the outer lobe, *d*. 4, the base, or pedicel, of the second maxillæ, or labium, the expanded terminal portion being drawn separately; *d* and *a*, two movable stout stylets representing, perhaps, the labial palpi; the lobe to which they are attached is multidentate, and adapted for seizing its prey; on the right side the two stylets are appressed to the lobe; *x*, represents, perhaps, the ligula; but we have not yet studied its homologies carefully; this part is attached to a transversely linear piece soldered to the main part of the labium; *y*, the 11th abdominal tergite, with its pair of conical anal stylets; *z*, the last tarsal joint and pair of long slender claws.

front. The thorax has greatly diminished in size, while the abdomen has become wider, and the limbs very long; and the numerous minute tubercles seen in the preceding stage have given origin to hairs. The dorsal vessel can now, for the first time, be seen. When in motion, the resemblance to a spider is most striking. The nervous ganglia are from one fourth to one fifth as wide as the abdomen itself, and are connected by two slender commissures. The flow of blood to the head, and the return currents through the lacunar, or venous circulation along the sides of the body are easily observed. The vessels were not crowded with blood discs, the latter being few in number, only one or two passing along at a time. Two currents passing in opposite directions were observed in the legs.

The young larva differs remarkably from the mature larva (which for the most part differs from the pupa (cut 4) only in the smaller eyes and absence of the rudiments of wings) in the much longer legs and shorter abdomen, and in the presence of the deciduous tubercles (cut 3, *c*) situated on the vertex of the head.

4.

Individuals were seen which were supposed to have undergone their first moulting, being nearly as large again as the freshly hatched larva, and with the abdomen a little longer.

The larvæ, after hatching, were not observed through their transformations. It is probable that, like the young Chloëon, which, according to Lubbock, moults twenty times before assuming the imago, or winged state, the young dragon-fly moults more than four or five times, the usual number in the insects with complete metamorphoses.

THE DEVELOPMENT OF PERITHEMIS.

During the summer of 1870, I had an opportunity of witnessing some steps in the development of *Perithemis domitia*, which show that in all respects the embryology of this genus is identical with that of the species of Diplax, and confirms the general accuracy of the drawings by Mr. Emerton, and my own observations. On a sunny day (July 28th), I observed a dragon-fly hovering over the surface of a pond, dipping its abdomen (the body being in a perpendicular attitude, with the wings in rapid motion) lightly into the water which just covered a piece of floating cow dung, and then fly off to return again and repeat the operation. Several dragon-flies were coursing over the small pond, and I am inclined to think that two or more dragon-flies pushed their eggs into this same mass of ordure. The dipping motion was the work of an instant; whether one, or a packet of eggs were deposited at a single dip of the abdominal tip I could not say, but from the arrangement of the eggs I should suppose they were deposited one by one at each dip of the abdomen.

Upon examining the piece of dung, which was soft, the upper side for a couple of square inches was seen to be covered with a jelly-like mass of thick consistency (thicker than the ropy mass enclosing the eggs of Diplax) which filled up the cavity in the piece of dung. The eggs were scattered through the mass several deep, and were not arranged in any order.

On examination the embryos were mostly in an advanced stage of growth, some having hatched, and it is accordingly probable that the dragon-flies had visited this favorite spot for oviposition for a period of two or three weeks.

The eggs are regularly oval and about one half as large as in Diplax, though of exactly the same form. The contents (observed with a 4-10 Zentmayer and A eye-piece) consisted of larger cells with more numerous minute ones, much as in the eggs of a species of Lecanium from the grape-vine which I was examining the same day.

Most of the eggs were provided with an acute tubercle like that figured on Plate 2, figure 13, *c*, and of the same form and relative size, being a little more than twice as long as the base is thick, and situated at the anterior end of the egg. It is transparent and evidently arises from the shell, beneath the layer of gum. I did not examine it under a higher power, but am inclined to think that it is the micropyle.

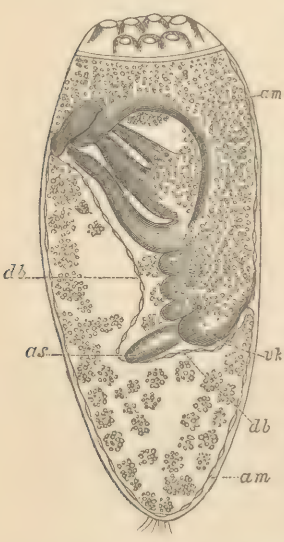
The egg is surrounded by a network of rudely hexagonal areoles, some being almost round, and others oblong; about twenty perfect areoles could be seen on the surface of the egg next to the eye. Similar areoles are described and figured by Dr. A. Brandt as surrounding the egg of Agrion and Calopteryx. He also states that Prof. R. Leuckart has described them in the eggs of *Æschna grandis* (Müller's Archiv, 1855, p. 204). This solid coating of gum is annoying to the observer, but in many eggs falls off. The chorion is slightly horn-colored, and a little more transparent than in Diplax.

While most of the eggs were well advanced I was fortunate enough to observe the primitive band in one egg. Like that of Agrion and Calopteryx, and of the Lecanium eggs then under observation, it was internal to the yolk, but situated nearer to one side of the egg than the other. The next stage observed corresponds exactly to that indicated by Plates 1, 2, figures 8, 8*a*. The appendages both of the head and thorax were as indicated in the figures referred to, the joints of the limbs not being formed. The yolk-sac was confined to the back and subdivided into several large compartments filled with the ordinary yolk-cells.

On squeezing out an embryo just ready to hatch, it exactly repeated the form represented by Plate 2, figure 9, the division between the front-head, or cephalic lobes, and the second maxillary segment, being well marked. The tracheæ and the nervous cord were the same in appearance.

The only difference between the recently hatched larva and that of Diplax was, that the head of the former is squarer, the eyes being more prominent. The nervous ganglia are large and rounded, and connected by two short, broad commissures. The heart is tubular, with the valves corresponding in position to each suture of the body. The valves are long, oblique at a slight angle to the walls of the vessel, and, when closed, form an acute v. The two valves approach each other at each pulsation, nearly but not quite closing together, like the wires in a certain kind of rat-trap. The pulsations were quite irregular, sometimes but a single, rather long, oval blood globule passing slowly along; at other times a number of globules pass along together. At times four or five beats intervened without the passage of a single globule. Indeed much fewer globules were apparently sent forward through the heart than flowed back by the lateral pair of veins, along which they passed obliquely.

5.*



The larva is active, swimming up and down in the water, and feeds on large infusoria, catching them by suddenly dropping its labial mask, and retaining its victim in its grasp by its mandibles. Some it rejected, while others it swallowed with a relish.

Comparison with the Embryo of Calopteryx and Agrion.—Since the observations on Diplax were made, and abstracts read at the meeting at Burlington (August, 1867) of the American Association for the Advancement of Science, and published in the "American Naturalist" for February, 1868, and in the "Proceedings of the Boston Society of Natural History" (vol. xi) for January 22d, 1868, I have received, through the kindness of Dr. Alexander Brandt,† of St. Petersburg, his admirable paper on the embryology of Agrion, Calopteryx, and certain Hemiptera.

Brandt's studies were directed chiefly to the development of the embryonal membranes. His conclusions are: "1st. Calopteryx and Agrion are developed according to the type of the development as shown by Metschnikow to exist in the Hemiptera, namely, the germ or primitive band is internal to the yolk.

"2d. In those insects with an internal germ we need to distinguish an embryonal membrane, which is divided into a visceral and a parietal layer.

*The accompanying figure (cut 5), from Professor Nicolaus Melnikow's "Beiträge zur Embryonalentwicklung der Insekten" (Wiegmann's Archiv für Naturgeschichte, 1869, p. 136), of the embryo of *Pediculus capitis*, will show plainly the relations of the parietal and visceral layers to the germ; *vk*, indicates the cephalic lobes (scheitelplatten), the rudimentary appendages of the head and thorax being situated in the middle and posterior pole of the egg, the embryo being about to revolve in its egg; *am*, is the parietal (amnion), and *db*, the visceral layer; *as*, the antennæ.

†Beiträge zur Entwicklungsgeschichte der Libelluliden und Hemipteren mit besonderer Berücksichtigung der Embryonalhülle derselben. Von Alexander Brandt, Jun. Read October 29th, 1868, before the Académie Impériale des Sciences de St. Petersburg. 4to, pp. 33. With 3 plates. St. Petersburg, 1869.

"3d. The visceral layer (veiled or plaited layer of Metschnikow) does not become united with the extremities, but enters, together with the parietal layer (amnion of Metschnikow), into the formation of the yolk sac.

"4th. The formation of the yolk sac, together with the revolution or turning of the embryo on its transverse axis, consists in an independent contraction of the parietal layer of the embryonal membrane."

As my attention was directed to morphological points, we can only infer from the few data given above that Diplax and Perithemis have the same arrangement of the embryonal membranes, and that these membranes later in the life of the embryo form the yolk sac, through the contraction of the parietal layer of the embryonal membrane, as in Agrion, Calopteryx, and certain Hemiptera.

As regards the changes of the embryo after the rudiments of the appendages have appeared, they seem in Diplax and Perithemis to be the same as in Calopteryx and Agrion. My figures 2, 2*a* may be compared with Brandt's figure 11; figure 4 with Brandt's figure 12. The embryo of Diplax is much thicker and shorter, corresponding to the shorter, more ovate egg. The attitude of the germ during its turning in the egg is identical with that of Agrion and Calopteryx. Finally, Brandt's figure 19 may be compared with my figures 8, 8*a*, and 9, the yolk now being confined to a small area on the back of the embryo, which is now segmented and nearly ready to hatch, the claws being indicated, the eyes formed, the appendages partly jointed, and otherwise much as in the larva.

THE DEVELOPMENT OF ISOTOMA.

The following fragmentary notes and rather rude drawings are published simply because any knowledge, however slight, of the mode of development of the Thysanura is very desirable at this time, as bearing both on the principles of embryology of insects and the morphology of this interesting and difficult group.

All that we know of the embryology of the Thysanura are some "unsatisfactory observations" on Podura recorded by Nicolet (Dohrn, Ent. Zeitung, Stettin 1869, p. 244), and a figure of the embryo of "Podurella" in Agassiz and Gould's "Principles of Zoology," figure 110, p. 144 (Edition of 1854). This represents the embryo just ready to hatch. Dr. Dohrn has evidently gathered enough from Nicolet's observations to determine him to place Podura among those insects in which the germ, or primitive band, is external to the yolk (*Insecta ectoblasta*).

Sir John Lubbock, in his memoir "On the Generative Organs, and on the Formation of the Egg in the Annulosa" (Phil. Trans. London, 1861, p. 595), has described the ovarian egg of *Petrobius maritimus*, and its mode of formation. The egg is compound, as in the insects generally; the "original epithelial, or at least ovarian cell, which becomes the

whole egg in Argulus, Limulus, Argas, Mermis, etc., forms in other cases only the Purkingean vesicle," the eggs of Limulus, etc., being, according to Lubbock's view, simple. He states that "the mature egg is elongated fusiform, about $\frac{3}{200}$th of an inch in length, and enclosed in a tough, somewhat transparent chorion. The yolk consisted as usual, of a viscid substance, containing fine granules and oil globules, varying up to $\frac{1}{1000}$th of an inch in diameter."

The eggs of *Isotoma Walkerii* were found by Mr. C. A. Walker, at Chelsea, under the bark of an apple tree, on the 25th of April, 1870. They were either laid singly or in small scattered groups on the damp under surface of the bark. The eggs are spherical, glistening white, with the chorion very transparent. They measure .0625 of an inch in diameter. At the date above mentioned many of the embryos had hatched, as the young were found in various stages of growth. They continued to hatch until May 6th. Numerous eggs were observed in which the blastoderm had not yet been formed. In these, amid a mass of minute granules, floated from two to four large oil globules (Pl. 3, fig. 2, *c*), the largest of which was one fourth the diameter of the egg itself, while there were numerous smaller globules measuring about one fourth the diameter of the largest cells.

The earliest stage I was able to observe (Pl. 3, figs. 1, 2) was the period of formation of the primitive band. I could not detect any eggs with blastodermic cells, or a blastoderm fully formed. Figure 2 represents the primitive band lying upon the outside of the yolk, next to the chorion, and divided into the external tegumental layer (*t*) and the inner, or muscular, layer (*m*). The two ends of the primitive band meet at *a*, the band thinning out so as to be of an imperceptible thickness just before *a* (fig. 1), where there is a clear space and an infolding (*a*) of the primitive band, which seems to be the place of meeting of the anterior and posterior end of the germ. A little later the fold grows deeper (as at *b*, fig. 2), and *a* seems to indicate the rudiments of the cephalic lobes. The exact mode of origin of these lobes (Scheitelplatte of Zaddach) I did not observe.

At a more advanced period of development, the primitive band, now more properly speaking, the primitive body-walls, is clearly defined, and is more homogeneous, the small cells previously scattered through its substance (as in fig. 2) having disappeared. This stage is signalized by the appearance of the primitive arthromeres, or segments of the body (*protozoonites* of Claparède). They originate just as they do in the Phryganidæ, according to Zaddach. They arise six in number (fig. 3), representing probably three cephalic and three thoracic segments (unless the fourth is the 2d maxillary arthromere, which more extended observations may prove to be the case). It will be noticed that they arise on the opposite side of the egg from the fold *a*, so that the cephalic lobes, (*pl*) extend from *a* around to I. The central portion, or muscular layer

of the egg, is now more homogeneous than before, the fat globules having disappeared in the centre of the egg. Plate 3, figures 4 and 5, represent the germ farther advanced and the budding out of the appendages.

The cephalic lobes are, as in figure 5, quite clearly indicated, and the rudimentary appendages, in most cases, well shown. At about this period the yolk sac is more circumscribed than before in the germ. Whether there is an internal division of the embryonal membrane (visceral membrane) which forms the yolk sac, as in Agrion and the Hemiptera, I was not able to determine. The outer layer ("amnion," or parietal layer), which surrounds the embryo, I did not at this stage observe, but as soon as the appendages are formed, as in figure 8, the chorion bursts on slight pressure, and the embryonal membrane is readily detected, enveloping the embryo, like the "larval skin" of many crustacea.

At the period indicated by figure 6 the dorsal walls (tergites) of the arthromeres are closed in, and the rudiments of the spring (figs. 6 and 7, *sp*) appears. It is liable to be mistaken for the antennæ (I) so large and well developed is it. It is evidently in all respects, both in its origin from the under side of the penultimate segment of the abdomen, and in its form, homologous with the cephalic and thoracic appendages.

In figure 7 the mandibles are just behind, and but little smaller than the antennæ (I), and in a vertical view (fig. 9) of the embryo when somewhat older, a pair of tubercles (II) are seen next to the rudimentary antennæ (I), which are probably the rudiments of the mandibles. In figure 10, *i* indicates the position of the rudiments of the alimentary canal; the yolk-cells composing it are much smaller than those scattered over the other portions of the body, and in the appendages. Figure 11 shows the antennæ of much greater length than before, with the rudiments of the articulations scarcely indicated.

At a later period the antennæ, especially, seem to show traces of articulations, and have grown much longer, while the end of the abdomen is divided deeply by the median furrow into two lobes. The mandibles (II) and first maxillæ (III) are distinct. I was unable at this or any other period to discover any traces of the second maxillæ. Though existing in a very rudimentary state in the adult I could not detect them after repeated attempts, but do not doubt but that a more skilled observer would have made them out. Indeed it is a most difficult thing to discover their rudiments in the adult; I failed, at the time these observations were made, to detect them, though since then I have succeeded in making out their structure and relation to the surrounding parts of the mouth.

The cephalic lobes are very distinct, and posteriorly defined by a slightly marked suture from the postoral portion of the head. They are deeply cleft by the median line of the body. There are no indica-

tions of the basal tergites of the head, the segments to which they belong being not yet differentiated from the thorax.

A later period (figs. 13, 13*a*) is characterized by the differentiation of the head as a distinct region of the body, the posterior portion, or postoral division of the head (including the mandibular and first maxillary arthromeres) uniting with the cephalic lobes to form the head, which is distinctly seen to move freely on the thorax. The ocelli are eight in number, and arranged obliquely in pairs, being situated on an elongated oval area just above the base of the antennæ. The two pairs of rudimentary postoral appendages, comprising the mandibles and maxillæ, are now greatly increased in size, both of much the same size and form, except that the hinder pair are divided by a slightly marked articulation, which is not observable in the mandibles. The basal division of the maxilla probably represents the cardo and stipes together, the distal articulation representing the future palpus, galea and lacinia. When seen in a front view we can better observe the relations of these organs to the labrum. This latter partially overlaps the mandibles on their inner edge, while the maxillæ are more external, though partly covered in front by the mandibles.

The front of the head is so entirely different from what it is in the adult, that certain points demand our attention. It is evident that at this period the development of the insect has gone on in all important particulars much as in other insects, especially the Neuropterous Mystacides as described by Zaddach. The head is longer vertically than horizontally, the frontal, or clypeal, region is broad, and greater in extent than the epicranio-occipital region. The antennæ are inserted high up on the head, next the ocelli,* falling down over the clypeal region. The clypeus, however, is merged with the epicranium, and the usual suture between them does not appear distinctly in after life, though its place is seen in figure 13 to be indicated by a slight indentation. The labrum is distinctly defined by a well marked suture, and forms a squarish knob-like protuberance, and in size is quite large compared to the clypeus. From this time begins the process of degradation, when the insect assumes its Thysanurous characters, which consist in an approach to the form of the Myriapodous head, the front, or clypeal region being reduced to a minimum, and the antennæ and eyes brought in closer proximity to the mouth than in any other insects.

That other most essential Thysanurous characteristic, the spring, is now fully formed. It arises as a thick tubercle from the sternite of the penultimate segment of the abdomen, and subdivides into a pair of two-jointed finger-shaped prolongations.

The tip of the abdomen is deeply bilobate, the median line of the body being deeply impressed.

The final stage in the life of the embryo is just previous to hatching,

* The basal joint is not shown in fig. 13 *a*, but is well indicated in the side view of the embryo, fig. 13.

(figs. 14, 14*a*). At this time the animal lies with the body so curved that the tip of the abdomen just touches the mouth. The ocelli are situated on an irregular lunate spot. The mandibles and maxillæ are long, slender, blade-like, concealed within the head, so that the mouth is somewhat tubular, as it appears in a front view of the head. They move back and forth upon one another, and, in their relation to the head, may be compared with the base of the mandibles and maxillæ in the head of *Cimex lectularius* and *Coreus tristis.* At this period I could not detect any traces of a labium. The feet end in two claws, one being minute and very slender. Neither at this, nor in the larval state, could any traces of the tracheæ be observed, and I doubt whether they exist.

The embryo when about to hatch, throws off the eggshell and "amnion" (or "larva skin") in a few seconds. The larva is perfectly white, and is very active in its movements, running over the damp, inner surface of the bark. The larva (figs. 15, 15*a*, spring; 16, 16*a* under side of the head, showing the mandibles and maxillæ, II, III; 17, the same seen ventrally) is a little over one hundredth of an inch in length, and differs from the adult in being shorter and thicker, with the spring very short and stout; while the head is much rounded, and the antennæ are stout and thick. In fact the larva assumes the form of the lower genera of the family, such as Achorutes and Lipura, the adult more closely resembling Degeeria.

The larva after moulting retains its early form, and is still white. It is then two and a half hundredths of an inch in length. After a second moult the body becomes purplish, translucent, and in form much more slender, resembling the adult.

The eggs are laid and the young are hatched apparently within a period of from six to ten days.

The adult seems to be undescribed, and I take pleasure in naming it *Isotoma Walkerii*, after Mr. C. A. Walker through whose instrumentality I have been able to study its embryology.

It belongs to Nicolet's first section of the genus, of which the European *I. glacialis* is a type. It is .04 of an inch in length, and is dull yellowish snuff-green in color. The four-jointed antennæ have the third joint smaller and shorter than the second, which is larger than the first; the terminal joint is long oval, and equals in length the second and third together. The abdomen is broadest just before the end; the spring arises from a short stalk, while the fork is long and slender, the branches being bowed outward near the base. It was found in abundance in the spring, and during the past autumn in November and the following spring again, under the bark of the same tree.

Comparing the development of Isotoma with that of Mystacides, a Phryganidan, as worked out so thoroughly by Zaddach, the correspondence throughout the different stages is very striking, so that we may

feel warranted in saying that the formation of the germ, and the growth of the embryo of Isotoma is, in the most important points, almost identical with that of the Phryganidæ.

As in the Phryganidæ (assuming that Mystacides fairly represents the mode of development in the family generally), the Isotoma germ is an "ectoblast," *i. e.*, the primitive band is developed on the outside of the yolk, and my figures 1, 2 and 3 may be compared with Zaddach's figures 13–19. Melnikow in his "Beitrage zur Embryonalentwickelung der Insekten" in "Wiegmann and Troschel's Archiv," 1869, p. 148, describes the outer ("amnion" or parietal) and inner (faltenblatt, or visceral) membrane of Mystacides, which Zaddach had overlooked. The parietal layer of Isotoma was readily perceived, but the visceral layer was not detected. The embryo, at the time represented by figure 12, may be compared with Zaddach's figure 40. At this period the dermal walls of the posterior portion of the head (including the mandibular and maxillary segments and thorax) have not been completed. The yolk also has been more completely absorbed, and the abdomen is doubled upon itself; this is due to the great length of the germ of Mystacides as compared with that of Isotoma, rather than to any important structural difference. A succeeding step, represented by figures 13 and 13*a*, may be compared with Zaddach's figure 52 (as shown in the adjoining cut 6). The position of the two embryos is the same, though in Isotoma, the development of the antennæ has been accelerated over that of the mandibles and maxillæ, where in Mystacides they are coördinated in their development with the last named appendages, otherwise the two embryos are much alike. The growth of the young Isotoma henceforth remains almost at a standstill; and there is only an elaboration of the articulations, the formation of claws, of hairs, and a slight change in the form of the head. Much greater changes are effected after this stage in Mystacides, *i. e.*, the mouth-parts and antennæ undergo a greater modification, the legs are greatly elongated and the different pairs vary greatly in form; the tracheal system is perfected, and the tubercles on the basal ring of the abdomen, by which it is retained in place in its case, are developed, so that there is a vast difference between the freshly-born young of the two insects; the one form having gone on in the natural course of development, the other being, in many very essential points, retarded.

6.

An interesting point in the embryology of Isotoma is the homology of the spring. Though its earliest development was not observed, it is evidently homologous with the third pair of blades comprising the unjointed ovipositor of the higher insects, and seems to be homologous with the legs and cephalic appendages.

The question naturally arises whether after all, contrary to my own conclusions,* the three pairs of non-articulated tubercles, which form the ovipositor of the winged hexapodous insects, may not be modified abdominal limbs, and homologous with the three pairs of spinnerets of the spiders, and the abdominal feet of Myriapods. Another point, that I have been led by these and other embryological studies to reconsider, is the important question whether the eyes of insects (including spiders and Myriapods) are homologues of the limbs, and are developed on separate cephalic segments. My attention was called forcibly to reconsider this point, by the embryo of Limulus, in which a pair of ocelli are situated indubitably on the first segment, and the compound eyes on the third segment of the cephalothorax, each of these segments bearing a pair of limbs! Evidently they are, in Limulus, modified dermal sense-cells, and developed without reference to whether the segment bears limbs or not.

In certain mites, as Hydrachna, Pontarachna, Thalassarachna, and probably all the Hydrachnidæ, the ocelli are situated over the second pair of legs at a considerable distance behind the head. In a genus of Annelids (Polyopthalmus) organs of sight are developed on each ring of the body, or, as in certain Planarians, scattered irregularly over the body. In the embryo of Isotoma and Diplax the ocelli are evidently developed on the antennary segment, as they are epithelial cells primarily situated on the cephalic lobes, which seem to form the tergite of the antennary segments. With this view, the supposition I have expressed (led thereto by the generally received opinion of Milne-Edwards, Dana, and others, that the eyes of insects and Crustacea represent limbs and therefore demand separate segments) seems incorrect. Accordingly, we seem forced to the belief that the head of the hexapodous insects consists of but *four* segments, *i.e.*, the second maxillary, first maxillary, and mandibular segments, situated behind the mouth-opening, and the antennary, or first and preoral segment, situated in front of the mouth. The cephalic plates, which fold back upon the head, forming the main expansion of the insectean head, is apparently the tergum of the antennary segment. The clypeus and labrum are apparently differentiated from the cephalic lobes, and thus seem to form a portion, or fold, of the antennary segment. These cephalic lobes in the Arachnids are described and figured by Claparède as folding back on top of the mandibular and maxillary segments, bearing ocelli and forming the anterior wall of the mouth. The upper part of the head of an insect is, then, largely tergal, rather than pleural as previously stated by me.

*Proceedings of the Boston Society of Natural History. Vol. 11. p. 393. 1868.

EXPLANATION OF PLATES.

Plates 1, 2. Embryology of Diplax.

Figures 1, 1*a*. Side and front view of the egg after the blastoderm has probably formed; 2*b*, another egg before primitive band has been formed.

Figure 2. Lateral, and 2*a*, ventral, view of the embryo; *pl*, cephalic lobes; I, antennæ; II, mandibles; III, first maxillæ; IV, second maxillæ.

Figure 3. Egg enclosed in a gelatinous capsule.

Figure 4. Embryo farther advanced; *e*, eyes; *ab*, abdomen.

Figure 5. A later stage; *c*, clypeus; *st*, sternum; *pat*, temporary postabdomen; *i*, rudiments of intestine; t''', tergites of abdomen.

Figure 6. Revolution of the embryo, view from behind; 6*a*, side view; 1–11, the eleven segments, or arthromeres, of the abdomen; 6*b*, the embryo lying across the egg, side view.

Figure 7. The embryo a little older, and lying across the egg; 7*a*, the eye in its relation to the appendages of the head.

Figure 8. Embryo nearly ready to hatch, ventral view; 8*a*, the same seen laterally; 8*b*, front view of the head, showing the labium with the lateral terminal spines.

Figure 9. An embryo removed from the egg and straightened out; 1–3, the three anterior cephalic segments; 4, the fourth, or second maxillary, segment of the head; *t*, main trachea; *x*, respiratory plexus of tracheæ surrounding the intestine; *n*, nervous system.

Figure 10. An embryo a little farther advanced, the labium being a little shorter.

Figure 11. An embryo still farther advanced, the labium (IV) being still shorter.

Figure 12. An embryo showing the mode of origin of the tracheæ.

Figure 13. An egg showing the acute tubercle (*c*), supposed to be the micropyle.

Figures 14, 14*a*. An embryo just previous to hatching.

Plate 3. Embryology of Isotoma.

Figure 1. Portion of egg showing the fold *a*, in the primitive band. The lettering is the same in all the figures.

Figure 2. An egg a little farther advanced; *a*, fold; *b*, much deeper than in fig. 1; *t*, tegumental; *m*, muscular layer of the primitive band; *c*, large yolk cells.

Figure 3. The primitive band fully formed, with the protozoonites, I, II, III, being the rudiments of the antennary, mandibular, and first maxillary segments; V – VIII, the three thoracic segments; *a*, the fold, indicating where the two ends of the body meet; *pl*, the cephalic lobes.

Figure 4. The same farther advanced.

Figure 5. The same still farther advanced.

Figure 6. The segments of the body completed; *pl*, the cephalic plates; I, antennæ; *sp*, the rudiments of the spring.

Figure 7. Another egg, with the antennæ and spring in view, and probably the mandibles. The yolk mass is more circumscribed than before.

Figure 8. Tergal view of the germ, with the chorion (*ch*) broken, showing the embryo surrounded by the parietal membrane or larval skin (*am*).

Figure 9. The embryo seen tergally, farther advanced.

Figure 10. Showing the antennæ arising from beneath the cephalic lobes; and the three pairs of legs.

Figure 11. An embryo a little farther advanced, the antennæ being divided into joints.

Figure 12. An embryo much farther advanced, showing the cephalic plates distinctly separated from the posterior portion bearing the mandibles (II) and first maxillæ (III), which have not yet become differentiated from the posterior portion of the body.

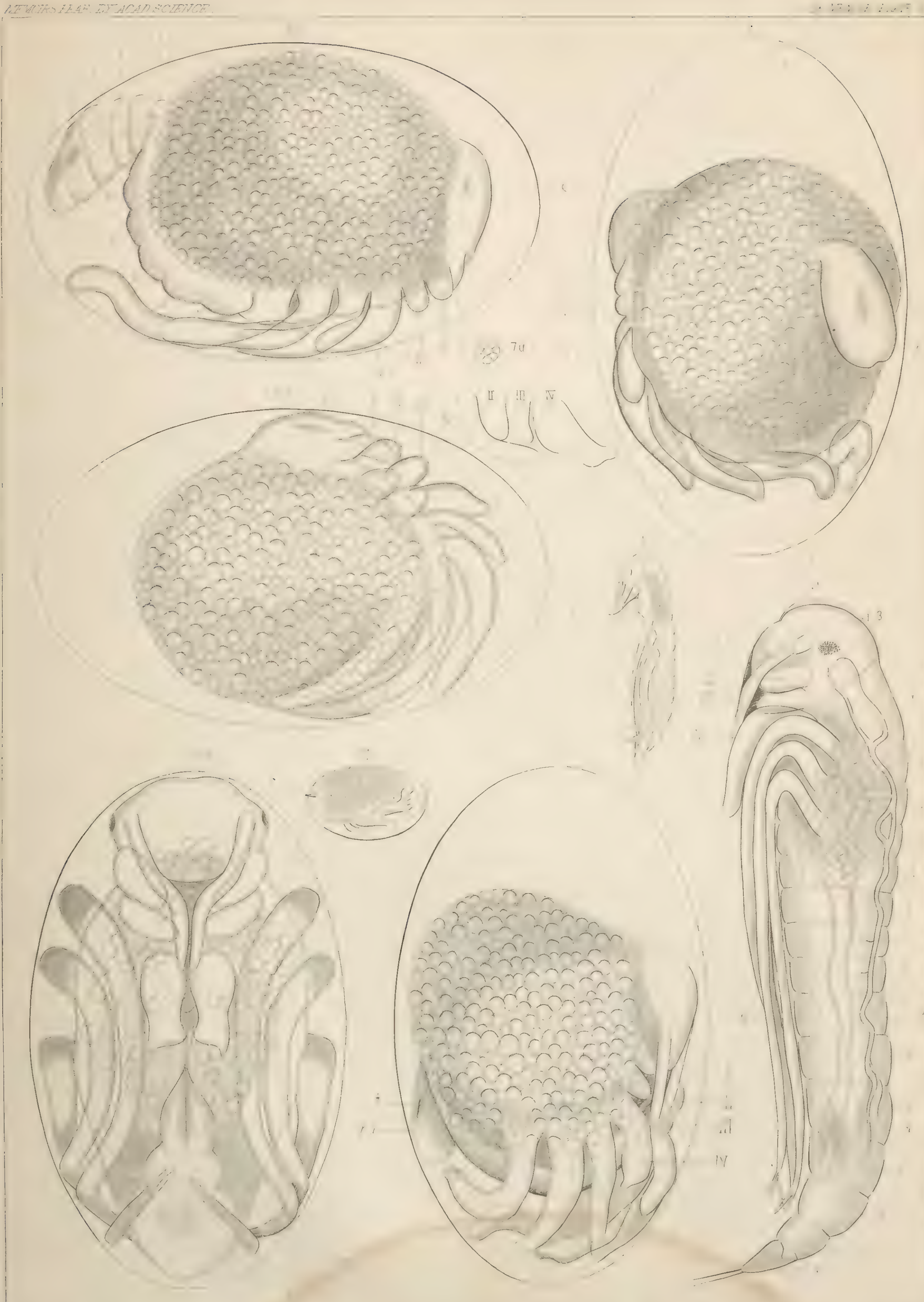
Figures 13, 13*a*. Side view of an older embryo showing the eyes, and labrum (*l*) differentiated from the clypeus; and the three-jointed spring and bilobate extremity of the abdomen.

Figures 14, 14*a*. The embryo just ready to hatch, the tip of the abdomen just meeting the mouth; 14*b*, front view of the head showing the mandibles and maxillæ.

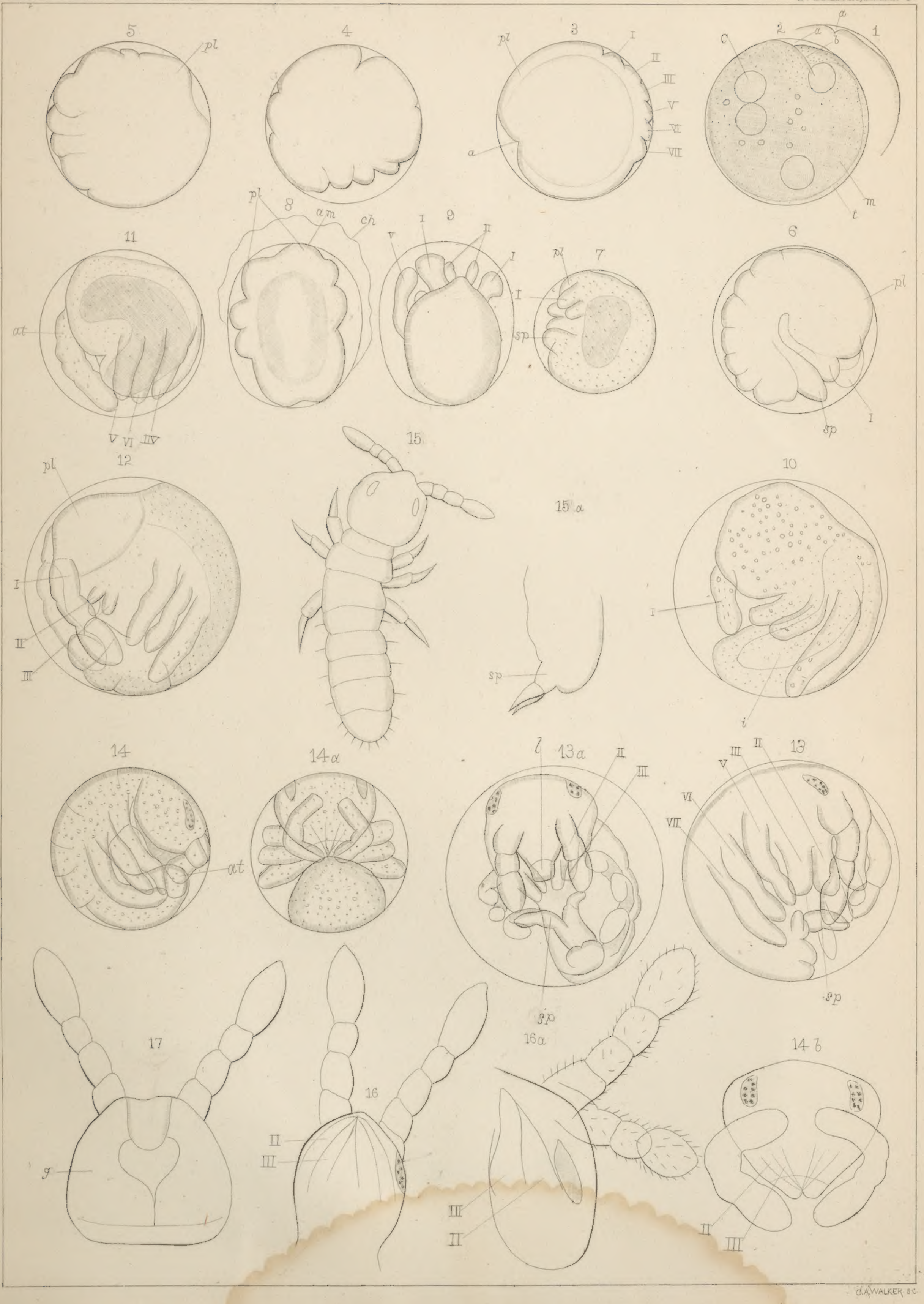
Figure 15. Freshly hatched larva; 15*a*, spring.

Figures 16, 16*a*. Under side of head showing relative position of the mandibles and maxillæ.

Figure 17. The under side of head showing the gular area.



PACKARD'S MEMOIR ON THE DEVELOPMENT OF INSECTS.



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